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Climate patterns as predictors of amphibian species richness and indicators of potential stress

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Amphibians occupy a range of habitats throughout the world, but species richness is greatest in regions with moist, warm climates. We modeled the statistical relations of anuran and urodele species richness with mean annual climate for the conterminous United States, and compared the strength of these relations at national and regional levels. Model variables were calculated for county and subcounty mapping units, and included 40-year (1960-1999) annual mean and mean annual climate statistics, mapping unit average elevation, mapping unit land area, and estimates of anuran and urodele species richness. Climate data were derived from more than 7,500 first-order and cooperative meteorological stations and were interpolated to the mapping units using multiple linear regression models. Anuran and urodele species richness were calculated from the United States Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) National Atlas for Amphibian Distributions. The national multivariate linear regression (MLR) model of anuran species richness had an adjusted coefficient of determination (R^2) value of 0.64 and the national MLR model for urodele species richness had an R^2 value of 0.45. Stratifying the United States by coarse-resolution ecological regions provided models for anurans that ranged in R^2 values from 0.15 to 0.78. Regional models for urodeles had R^2 values ranging from 0.27 to 0.74. In general, regional models for anurans were more strongly influenced by temperature variables, whereas precipitation variables had a larger influence on urodele models.

INTRODUCTION

Amphibian populations appear to be declining worldwide (HOULAHAN et al., 2000; CAREY et al., 2001; YOUNG et al., 2004). A number of possible causes of decline have been proposed including changes in climate (e.g., POUNDS & CRUMP, 1994; DONNELLY & CRUMP, 1998; POUNDS et al., 1999), increased UV radiation (e.g., ALFORD & RICHARDS, 1999; BLAUSTEIN et al., 2003), habitat loss/fragmentation/alteration (e.g., FAHRIG et al., 1995,

DEMAYNADIER & HUNTER, 1998; KRZYSIK, 1998; COLLINS & STORFER, 2003), introduction of nonindigenous competitive species (e.g., HAYES & JENNINGS, 1986, ROSEN & SCHWALBE, 1995, FISHER & SHAFFER, 1996; KIESECKER & BLAUSTEIN, 1998; LAWLER et al., 1999), occurrence of contaminants (e.g., BERRILL et al., 1993, BONIN et al., 1997; DAVIDSON et al., 2002, HAYES et al., 2002), exposure to pathogens (e.g., LAURANCE et al., 1996, KIESECKER & BLAUSTEIN, 1999) and over-harvesting (KOONTZ, 1992; LANNOO, 1996) Many herpetologists believe that combinations of stresses are being placed on amphibian populations (GREEN, 1997; BRITSON & THRELKELD, 2000; COLLINS & STORFER, 2003; LANNOO et al., 2003; LITTLE et al., 2003).

There is widespread acknowledgment that the global climate is changing (HOUGHTON et al, 2001). Changes in land cover may also affect climate by altering the physical properties of the land surface (HAYDEN, 1998; PIELKE et al, 1999, 2002) Short- and long-term changes in climate have the potential to affect the ranges of individual amphibian species and hence species richness in any given locality (THOMAS et al., 2004) Climatic conditions not only directly stress amphibian populations (DODD, 1997, POUNDS et al., 1999, CORN & MUTHS, 2002), but also may influence their resistance to disease or their ability to withstand attacks by environmental pathogens (CAREY & ALEXANDER, 2003). Water availability, air temperature and relative humidity can influence amphibian breeding, development, foraging, mobility, calling, immune response and habitat availability (DONNELLY & CRUMP, 1998, GIBBS & BREISCH, 2001). Climate also can influence the spread of amphibian pathogens (DASZAK et al, 2003; JOHNSON & CHASE, 2004).

Amphibians have a long (~350 million years) history of survival under extremes in global climate (CAREY & ALEXANDER, 2003), yet their life histories (DUELLMAN, 1999*a*) suggest that individual amphibian populations may be vulnerable to short-term variations in climate. Amphibians occupy a range of habitats throughout the world, but species richness is greatest in regions with moist, warm climates (DUELLMAN, 1999*b*) Other natural factors that can affect amphibian species richness include historical lineages, barriers to migration, interspecies competition and the availability of food, shelter and breeding sites.

OBJECTIVES AND SCOPE

This research assesses the degree to which average climatic conditions in the conterminous United States over the last four decades explain historical patterns of amphibian species richness. The primary objectives of the research were to model the statistical relations of anuran and urodele species richness with mean annual climate for the conterminous United States, and to compare the strength of these relations at national and regional levels. Trends in climatic conditions during this period were also evaluated to determine if they might be leading towards more stressful conditions for amphibians (e.g., decreases in available breeding habitat, shortening of breeding season).

There were limitations or biases implicit in the datasets used for these analyses. First, the species occurrence records incorporated into the ARMI National Atlas for Amphibian Distributions were not associated with an explicit time period and are best described as an historic compilation of occurrence records. Second, the species richness estimates were compared to climate statistics averaged for 1960-1999. Climate from this time period may not match longer-term averages or averages from other time periods. Third, the species richness estimates [http //www.mp2-pwrc usgs.gov/armiatlas/] were based on mapping units (counties/subcounties) that are not of uniform size, resulting in the potential for an inherent bias towards a larger number of species occurring in larger counties. Fourth, neither the weather stations nor the spatial variability of weather were uniformly distributed across the United States, so the quality of information varied from mapping unit to mapping unit Fifth, the mean elevation was used for each mapping unit, but the concept of average elevation may not be useful in mountainous areas. No attempt was made to account for the patchiness of the distribution of species within a county/subcounty (KIESTER, 1971), because such data do not exist for most of the United States, and no attempt was made to account for the effect of climate variation on species that prey upon amphibians or that amphibians consume. Despite these limitations, and because strong relationships between climate and ecosystem development are widely recognized (WALTER, 1973; FORMAN & GODRON, 1986; MONSERUD & LEEMANS, 1992), it was appropriate to expect that relations between climate and amphibian species richness would emerge from the analysis.

METHODS

SOURCE AND PROCESSING OF AMPHIBIAN DATA

Species richness estimates for anurans and urodeles were derived from the ARMI National Atlas for Amphibian Distributions (hereafter called "atlas") [http.//www.mp2-pwrc usgs.gov/armiatlas/], which uses a combination of counties and subcounties as a spatial framework for documenting the geographic occurrence of the nearly 300 species of amphibians currently recognized in the United States (LANNOO et al., 2005). Counties are used as mapping units for all but five Western states (Arizona, California, Nevada, Oregon, and Washington), for which subcounties are used to help overcome the wide disparity in county sizes across the nation. The atlas is a compilation of both current and historic records of amphibian occurrences, bounded by no explicit time period. The records are from peer-reviewed scientific literature, museum vouchers, state and regional herpetological atlases, and other confirmed and validated observations. Data sources vary by state and are not standardized in their geographic precision Thus, some records in the atlas may represent assumed presence, as from a range map, whereas other records represent vouchered specimens with specific location information. Because the atlas database incorporates a county/subcounty coding system that follows Federal Information Processing Standards, a geographic information system (GIS) was used to link species occurrence records with a digital map of county and subcounty polygons [http://www census.gov/geo/www/cob/scale html]. Species richness was calculated for anurans and urodeles by tallying the number of species recorded as occurring within each map unit.

SOURCE AND PROCESSING OF CLIMATE DATA

Estimates of 1960-1999 mean annual and annual mean climate statistics were calculated from approximately 7,500 National Weather Service first-order and cooperative temperature stations, and 11,500 National Weather Service first-order and cooperative precipitation stations. First-order stations are operated by professional staff and report a comprehensive array of weather variables each hour. Cooperative sites are more numerous, but generally only make once-daily observations of a few weather variables (e.g., minimum and maximum daily temperature and precipitation). These data were extracted from the National Climate Data Center Summary of the Day Dataset and have been quality controlled by the National Climate Data Center (EISCHEID et al., 2000; CLARK et al., 2004). Estimates of mean annual and annual mean climate statistics (tab. 1) for each county/subcounty were calculated using multiple linear regression (MLR) models. The MLR method was used to distribute the climate statistics (dependent variable) calculated at each station to each county/subcounty based on the "XYZ" value (longitude X, latitude Y, and mean elevation Z, respectively) of the county/subcounty polygon centroid (HAY et al., 2000, HAY & MCCABE, 2002; HAY & CLARK, 2003). The MLR equation [1] was developed for each dependent variable (climate statistic, "CS") using the independent XYZ variables from a set of National Weather Service climate stations.

$$CS = b_1 x + b_2 y + b_3 z + b_0 \quad [1]$$

The MLR equations were computed to determine the regression surface that described the spatial relations between the dependent CS and the independent XYZ variables. Equation [1] describes a plane in three-dimensional space with slopes b_1, b_2 and b_3 intersecting the CS axis at b_0. The best MLR equation for each CS did not always include all the independent variables.

To estimate the climate statistics for each county/subcounty (CNTY), the following procedures were followed: first, mean daily CS and corresponding mean XYZ values from a set of stations (STAMEAN) were used with the slopes of the MLR from equation [1] to estimate a unique y-intercept ($b_0$est, see equation [2]), and second, equation [3] was solved using the coefficients (b_1, b_2 and b_3) from equation [1], $b_0$est from equation [2], and the XYZ values of the CNTY.

$$b_0est = CS(STAMEAN) - (b_1 x(STAMEAN) + b_2 y(STAMEAN) + b_3 z(STAMEAN)) \quad [2]$$

$$CS(CNTY) = b_0est + b_1 x(CNTY) + b_2 y(CNTY) + b_3 z(CNTY) \quad [3]$$

The set of stations comprising the STAMEAN in each calculation were chosen from the 20 closest stations to the CNTY. Outliers (i.e., stations determined to be too far away from the data site or residing in another physiographic region) were not used in the STAMEAN calculation. The same MLR equations are used but the time series of mean daily CS and their corresponding mean XYZ values are obtained from station data to estimate a unique $b_0$est. Thus, the slope of the MLR for the CS remained constant, but the y-intercept changes based on the mean CS and XYZ values.

Trends in climate were calculated by comparing, through regression analysis, the annual mean CS in each county/subcounty against time (year). When the annual mean CS values

Table 1. 1960-99 Mean annual climate statistics and other independent variables used for this study.

Climate statistic or other variable (and definition)	Unit	Variable name
Mean annual precipitation intensity (average for all days)	millimeters per day	PRE
Mean annual precipitation minus mean annual potential evapotranspiration (average for all years)	millimeters per year	PRE-PET
Mean annual minimum temperature (average for all days)	degrees Celsius	TMN
Mean annual mean temperature (average for all days)	degrees Celsius	TME
Mean annual maximum temperature (average for all days)	degrees Celsius	TMX
Mean annual number of wet days (days with measured precipitation)	days per year	WDAY
Mean annual number of dry days (days without measured precipitation)	days per year	DDAY
Mean annual number of cold days (days with minimum temperatures below 0°C)	days per year	CDAY
Mean annual number of hot days (days with maximum temperatures above 35°C)	days per year	HDAY
Mean annual solar radiation (average for all days)	Langley's per day	RAD
Mean annual total winter degree days ({$T_{base} - T_{ave}$} where T_{base} = 3°C and T_{ave} = {$T_{max} + T_{min}$} / 2, zero if negative)	dimensionless	WDD
Mean annual total summer degree days ({$T_{ave} - T_{base}$} where T_{base} = 3°C and T_{ave} = {$T_{max} + T_{min}$} / 2, zero if negative)	dimensionless	SDD
Mean elevation	meters	ELEV
County area (total land area of county)	square kilometers	AREA

were missing or zero, no trend was calculated and a zero trend value was assigned to the county/subcounty. Simulated CS in each county/subcounty for the years 1960 and 1999 were calculated using the trend regressions and the mean annual CS. Hence, the differences between the simulated CS values for the two years represent the magnitude of the trend over the 40 year time period and not the differences between any two years of actual CS data.

Source and processing of elevation and area data

Two additional variables used to augment the climate information for each county/subcounty were average elevation and total land area. Elevation data were obtained from the USGS National Elevation Dataset [http://edc.usgs.gov/products/elevation/ned.html] and were projected from geographic coordinates referenced to the World Geodetic Survey of 1984 to an Albers equal-area conic projection using a bilinear interpolation, 1000-meter cell resolution, and the following parameters: ellipsoid – World Geodetic Survey of 1984, 1st standard parallel = 29 5°, 2nd standard parallel = 45.5°, central meridian = –96.0°, latitude of origin = 23.0°, and no false easting or northing Average elevation was calculated as the mean of all cells within each mapping unit. Polygons for map units [http://www census.gov/geo/www/cob/scale.html] were represented in an Albers equal-area conic projection using the same parameters as for the elevation data. Total mapping unit areas were determined from the county/subcounty polygons.

STATISTICAL METHODS

Multiple linear regression (MLR) models (HELSEL & HIRSCH, 1992) were developed using the SAS statistical software system (ANONYMOUS, 1990) to relate amphibian species richness to climate and location Dependent and independent model variables were standardized by subtracting the respective mean and dividing by the respective standard deviation. Standardized variables have equal weights in regression models, and the resulting model coefficients are proportional to their explanatory power in the models. "Best" and "stepwise" SAS regression procedures were used to screen potential models; however, neither method prevents correlated independent variables from entering the models. Multicollinearity among independent variables, as indicated by variance inflation factor (VIF) values greater than 10, can cause MLR model coefficients to be unrealistic in sign or magnitude (HELSEL & HIRSCH, 1992) When an MLR model contained an independent variable with a VIF value greater than 3, the independent variable was not used.

Two sets of regression models were developed. one set for the entire conterminous United States (including one model for anurans and one for urodeles), and one set for each of 10 coarse-scale ecological regions (ANONYMOUS, 1997) (fig. 1). Because the primary objective of this research was to determine the degree to which climate explains patterns of amphibian species richness, model selection was manually supervised to favor climatic terms and prevent highly correlated independent variables from entering the same model. The adjusted coefficient of determination (R^2) and root mean square error (*RMSE*) statistics were used to evaluate the predictive skill of the models for a particular region or the nation (ANONYMOUS, 1990; HELSEL & HIRSCH, 1992). The residuals between model and atlas estimates of species richness are used to compare the predictive capabilities of the national and regional models. Box plots are used to show the distributions of these residuals. The box plots show high and low outliers as circles. The central box extends from the 25th to 75th percentile of the data, and the box whiskers extend to the 5th and 95th percentiles.

RESULTS

NATIONAL REGRESSION MODELS

Anuran species richness ranged from a maximum of 26 to a minimum of 1 (fig 2a) The R^2 for the national anuran model (fig 3a) was 0 64 (tab 2), with an *RMSE* of 3 07 species. Mean annual temperature and mean annual precipitation (fig 1b) accounted for the largest

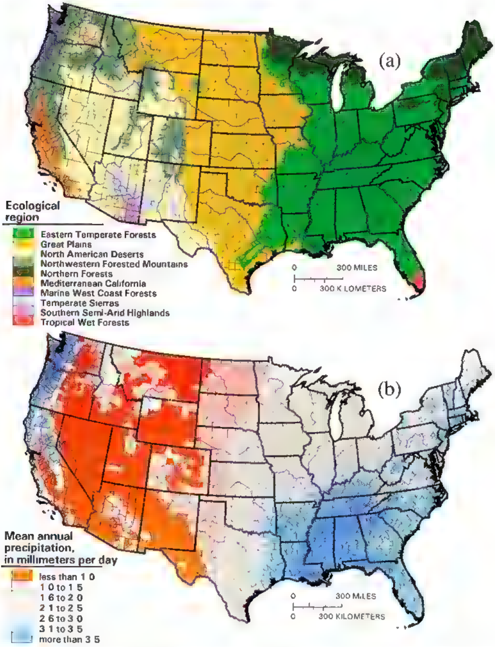

Fig. 1. – Maps showing in the conterminous United States (a) coarse-level ecological regions and State, county and subcounty boundaries, and (b) 1960-1999 mean annual precipitation.

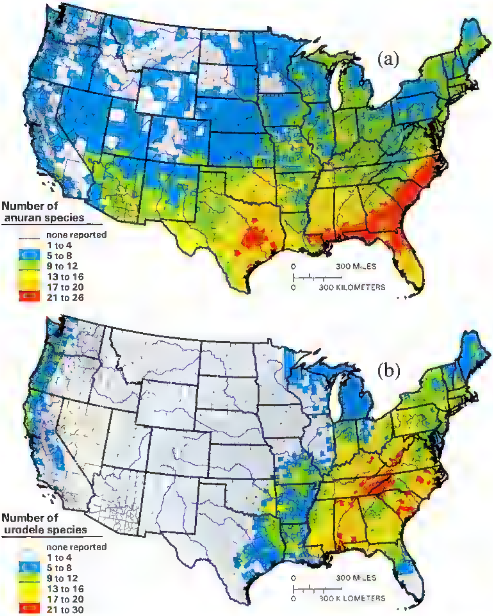

Fig. 2 Maps showing in the conterminous United States (a) anuran species richness and (b) urodele species richness, both from the Amphibian Research and Monitoring Initiative (ARMI) National Atlas for Amphibian Distributions.

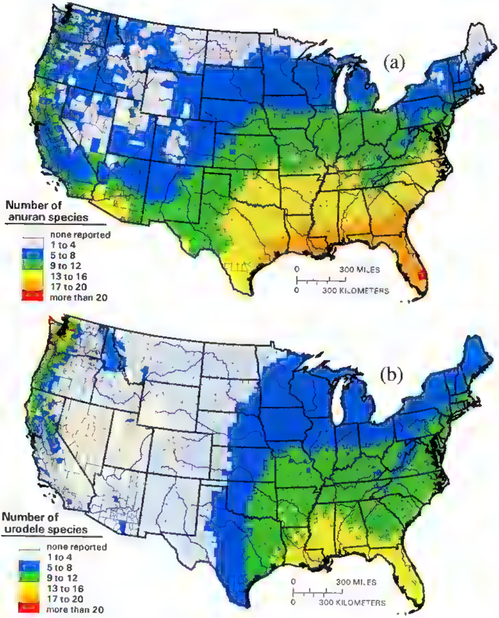

Fig. 3. – Maps showing in the conterminous United States the national regression model estimates of (a) anuran species richness and (b) urodele species richness.

Tab. 2. Best-fitting national and ecological region standardized regression models of amphibian species richness and adjusted coefficient of determination (R^2). NA, North American; NW, Northwestern. See tab. 1 for other abbreviations.

National or ecological Region	Regression model	R^2
	Anurans	
National	0.57*PRE + 0.56*TME - 0.49*PRE-PET + 0.07*ELEV	0.64
Eastern Temperate Forests	0.71*TMX – 0.21*ELEV + 0.10*WDAY + 0.07*AREA	0.63
Great Plains	0.78*TME + 0.18*PRE + 0.08*AREA – 0.07*ELEV	0.78
NA Deserts	0.79*TMX + 0.36*PRE + 0.22*AREA + 0.16*ELEV	0.47
NW Forested Mountains	-0.31*WDD - 0.27*ELEV + 0.25*AREA	0.23
Northern Forests	-0.35*ELEV + 0.34*CDAY + 0.33*PRE	0.15
Mediterranean California	0.45*ELEV – 0.41*CDAY + 0.39*RAD + 0.21*PRE	0.34
Marine West Coast Forests	0.34*TME + 0.22*ELEV + 0.14*AREA	0.25
Temperate Sierras	No statistically significant model.	-
Southern Semi-Arid Highlands	0.80*ELEV + 0.68*RAD – 0.68*CDAY	0.68
Tropical Wet Forests	Too few mapping units (5) to develop a model.	-
	Urodeles	
National	0.70*PRE - 0.24*PRE-PET + 0.11*TME - 0.05*ELEV	0.45
Eastern Temperate Forests	-0.65*WDD + 0.32*ELEV + 0.29*WDAY + 0.15*PRE-PET	0.50
Great Plains	0.55*PRE + 0.20* TME + 0.16*PRE-PET + 0.15*AREA	0.49
NA Deserts	-0.57*ELEV + 0.37*PRE + 0.20*AREA – 0.19*TME	0.27
NW Forested Mountains	0.55*PRE + 0.20*TME – 0.18*ELEV	0.60
Northern Forests	-0.67*WDD + 0.35*ELEV + 0.33*PRE	0.74
Mediterranean California	0.47*PRE – 0.43*WDD 0.34*TMX + 0.26*ELEV	0.50
Marine West Coast Forests	0.33*PRE + 0.31*TME + 0.23*ELEV + 0.22*RAD	0.40
Temperate Sierras	No statistically significant model.	-
Southern Semi-Arid Highlands	No statistically significant model.	-
Tropical Wet Forests	Too few mapping units (5) to develop a model	-

proportion of the variation (because they have the largest model coefficients, tab. 2), and were both positively associated with species richness. Mean annual precipitation minus mean annual potential evapotranspiration also accounted for a substantial proportion of the variation and was inversely associated with species richness. Mean mapping unit elevation accounted for a small proportion of the variation and was positively associated with anuran species richness. The national regression model overestimated anuran species richness along the Mississippi embayment and in parts of California, Florida, and Oregon. The model underestimated anuran species richness along the Atlantic coastal plain and in parts of Maine and Texas (fig. 2a, 3a).

Urodele species richness ranged from a maximum of 30 to a minimum of 0 (fig. 2). The R^2 for the national urodele model (fig. 3b) was 0.45, with an *RMSE* of 4.54 species. The national urodele model (tab. 2) used the same CS as the national anuran model, but the coefficient values were appreciably different. Mean annual precipitation accounted for the largest proportion of the variation and was positively associated with species richness. Mean annual precipitation minus mean annual potential evapotranspiration accounted for a smaller proportion of the variation and was inversely associated with species richness. The national regressions model overestimated urodele species richness in the central United States and in parts of Florida and Washington; and underestimated species richness in most of the Eastern United States except for Florida and Maine (fig. 2b, 3b).

Regional regression models

Separate regression models were developed for each coarse-resolution ecological region (fig. 1a) to evaluate regional differences in the strength of climate as a predictor of amphibian species richness. No models were developed for the Tropical Wet Forest ecological region, which was predominant only in five mapping units, and represented less than 0.3 % of the conterminous United States. The mean of anuran and urodele species richness for these five mapping units was used in place of a model.

Eastern Temperate Forests

The Eastern Temperate Forests ecological region was predominant in 1,789 mapping units, representing 31.8 % of the conterminous United States (fig. 1a). Anuran species richness in this ecological region ranged from 2 to 26, and urodele species richness ranged from 1 to 30. The R^2 for the Eastern Temperate Forest ecological region anuran model (fig. 4a) was 0.63, and the *RMSE* was 2.91 species. Mean annual maximum temperature accounted for the largest proportion of the variation and was positively associated with species richness. The Eastern Temperate Forest model overestimated anuran species richness in parts of Arkansas, Florida and Louisiana, and underestimated anuran species richness along the Atlantic Coastal Plain and in parts of Alabama and Indiana. The residuals (model estimate minus atlas estimate) for the Eastern Temperate Forest anuran model were much smaller than the residuals between national model and atlas estimates of anuran species richness in those same mapping units (fig. 5a; gray box plots are residuals from regional models and black box plots are residuals from national model in the same mapping units). The R^2 for the Eastern Temperate Forest ecological region urodele model (fig. 4b) was 0.50, and the *RMSE* was 3.78 species. The total of mean annual winter degree days accounted for the largest proportion of the variation, and was inversely associated with species richness. The Eastern Temperate Forest model overestimated urodele species richness in parts of Arkansas, Florida, Illinois, Louisiana and Texas, and underestimated urodele species richness along the Eastern coastal and inland plains and in parts of Alabama, Indiana and Kentucky. The residuals for the Eastern Temperate Forest urodele model were smaller than the residuals between the national model and atlas estimates of urodele species richness (fig. 5b).

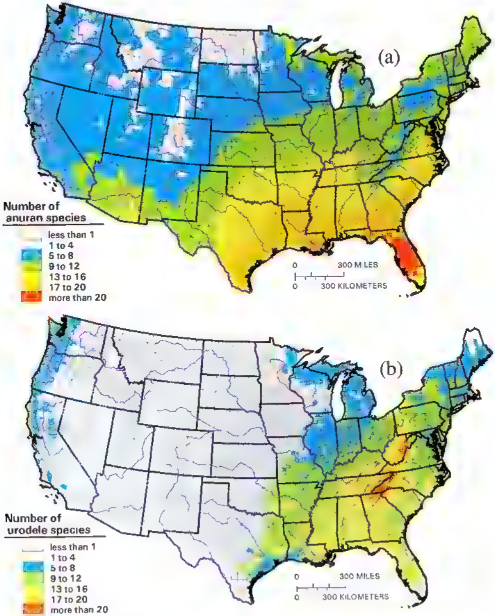

Fig. 4 Maps showing in the conterminous United States a compilation of regional regression models estimates of (a) anuran species richness and (b) urodele species richness.

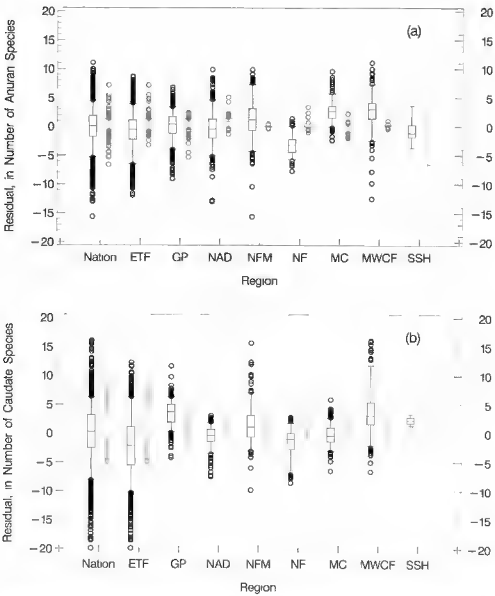

Fig. 5. – Box plots showing residuals (in species) between national regression model and atlas (black) and regional regressions models and atlas (gray) estimates of (a) anuran species richness and (b) urodele species richness. ETF, Eastern Temperate Forest; GP, Great Plains; NAD, North American Deserts; NFM, Northwestern Forestal Mountains; NF, Northern Forests; MC, Mediterranean California; MWCF, Marine West Coast Forests; SSH, Southern Semi-Arid Highlands.

GREAT PLAINS

The Great Plains ecological region was predominant in 837 mapping units, representing 28 9 % of the conterminous United States (fig. 1a). Anuran species richness in this ecological region ranged from 1 to 23, and urodele species richness ranged from 0 to 13. The R^2 for the Great Plains ecological region anuran model (fig. 4a) was 0 78, and the *RMSE* was 2.12 species. Mean annual temperature accounted for the largest proportion of the variation and was positively associated with species richness. The Great Plains model overestimated anuran species richness in parts of Kansas, Missouri and Nebraska; and underestimated anuran species richness in parts of North Dakota, Oklahoma and Texas. The residuals for the Great Plains anuran model were much smaller than the residuals between the national model and atlas estimates of anuran species richness (fig. 5a). The R^2 for the Great Plains ecological region urodele model was 0.49, and the *RMSE* was 1.10 species. mean annual precipitation accounted for the largest proportion of the variation and was positively associated with species richness. The Great Plains model overestimated urodele species richness in parts of Iowa, Kansas and Oklahoma, and underestimated urodele species richness in parts of North Dakota and Texas. The residuals for the Great Plains model were much smaller than the residuals between the national model and atlas estimates of urodele species richness (fig 5b)

NORTH AMERICAN DESERTS

The North American Deserts ecological region was predominant in 349 mapping units representing 19.8 % of the conterminous United States (fig. 1a) Anuran species richness in this ecological region ranged from 1 to 16, and urodele species richness ranged from 0 to 4. The R^2 for the North American Deserts ecological region anuran model (fig 4a) was 0.47, and the *RMSE* was 2 05 species. Mean annual maximum temperature accounted for the largest proportion of the variation and was positively associated with species richness. The North American Deserts model overestimated anuran species richness in parts of California and Utah, and underestimated anuran species richness in parts of Arizona and Texas. The residuals for the North American Deserts anuran model were much smaller than the residuals between the national model and atlas estimates of anuran species richness (fig 5a). The R^2 for the North American Deserts ecological region urodele model (fig 4b) was 0 27, and *RMSE* was 0 65 species. Mean mapping unit elevation accounted for the largest proportion of the variation and was inversely associated with species richness. The North American Deserts model overestimated urodele species richness in parts of California and Nevada, and underestimated urodele species richness in parts of California. The residuals for the North American Deserts urodele model were smaller than the residuals between the national model and atlas estimates of urodele species richness (fig. 5b).

NORTHWESTERN FORESTED MOUNTAINS

The Northwestern Forested Mountains ecological region was predominant in 289 mapping units, representing 9 1 % of the conterminous United States (fig 1a) Anuran species richness in this ecological region ranged from 1 to 8, and urodele species richness ranged from 0 to 12. The R^2 for the Northwestern Forested Mountains ecological region anuran model (fig. 4a) was 0.23, and the *RMSE* was 1.20 species. The total of mean annual winter degree days accounted for the largest proportion of the variation and was inversely associated with species richness. The Northwestern Forested Mountains model overestimated anuran species richness in parts of Colorado and Idaho, and underestimated anuran species richness in parts of Oregon. The residuals for the Northwestern Forested Mountains anuran model were much smaller than the residuals between the national model and atlas estimates of anuran species richness (fig. 5a). The R^2 for the Northwestern Forested Mountains ecological region urodele model (fig. 4b) was 0.60, and the *RMSE* was 1.77 species. mean annual precipitation accounted for the largest proportion of the variation and was positively associated with species richness. The Northwestern Forested Mountains model overestimated urodele species richness in parts of Washington, and underestimated urodele species richness in parts of Colorado and Oregon. The residuals for the Northwestern Forested Mountains urodele model were much smaller than the residuals between the national model and atlas estimates of urodele species richness (fig. 5b).

Northern Forests

The Northern Forests ecological region was predominant in 134 mapping units, representing 5.2 % of the conterminous United States (fig. 1a). Anuran species richness in this ecological region ranged from 5 to 10, and urodele species richness ranged from 1 to 15. The R^2 for the Northern Forests ecological region anuran model was 0.15, and the *RMSE* was 0.92 species. Mean mapping unit elevation accounted for the largest proportion of the variation and was inversely associated with species richness. The residuals for the Northern Forests anuran model were much smaller than the residuals between the national model and atlas estimates of anuran species richness (fig. 5a). The R^2 for the Northern Forests ecological region urodele model was 0.74, and the *RMSE* was 1.60 species. The total of mean annual winter degree days accounted for the largest proportion of the variation and was inversely associated with species richness. The residuals for the Northern Forests urodele model were slightly smaller than the residuals between the national model and atlas estimates of urodele species richness (fig. 5b).

Mediterranean California

The Mediterranean California ecological region was predominant in 277 mapping units, representing 2.1 % of the conterminous United States (fig. 1a). Anuran species richness in this ecological region ranged from 2 to 9, and urodele species richness ranged from 0 to 10. The R^2 for the Mediterranean California ecological region anuran model was 0.34, and the *RMSE* was 1.04 species. Mean mapping unit elevation accounted for the largest proportion of the variation and was positively associated with species richness. The residuals for the Mediterranean California anuran model were much smaller than the residuals between the national model and atlas estimates of anuran species richness (fig. 5a). The R^2 for the Mediterranean California ecological region urodele model was 0.50, and the *RMSE* was 1.46 species. Mean annual precipitation accounted for the largest proportion of the variation and was positively associated with species richness. The residuals for the Mediterranean California urodele model were smaller than the residuals between the national model and atlas estimates of urodele species richness (fig. 5b).

MARINE WEST COAST FORESTS

The Marine West Coast Forests ecological region was predominant in 219 mapping units, representing 1.1 % of the conterminous United States (fig 1a) Anuran species richness in this ecological region ranged from 3 to 6, and urodele species richness ranged from 2 to 10. The R^2 for the Marine West Coast Forests ecological region anuran model was 0.25, and the *RMSE* was 0 67 species. Mean annual temperature accounted for the largest proportion of the variation and was positively associated with species richness. The residuals for the Marine West Coast Forests anuran model were much smaller than the residuals between the national model and atlas estimates of anuran species richness (fig. 5a). The R^2 for the Marine West Coast Forests ecological region urodele model was 0 40, and the *RMSE* was 1 55 species. Mean annual precipitation accounted for the largest proportion of the variation and was positively associated with species richness. The residuals for the Marine West Coast Forests urodele model were much smaller than the residuals between the national model and atlas estimates of urodele species richness (fig. 5b).

TEMPERATE SIERRAS

The Temperate Sierras ecological region was predominant in 18 mapping units representing 1 1 % of the conterminous United States (fig 1a). Anuran species richness in this ecological region ranged from 8 to 14, and urodele species richness was always 1. No statistically significant model of anuran species richness could be developed from the available independent variables (tab 2). No model of urodele species richness was attempted since there was no variation in the dependent variable.

SOUTHERN SEMI-ARID HIGHLANDS

The Southern Semi-Arid Highlands ecological region was predominant in 17 mapping units representing 0 6 % of the conterminous United States (fig 1a) Anuran species richness in this ecological region ranged from 9 to 15, and urodele species richness was either 0 or 1 The R^2 for the Southern Semi-Arid Highlands ecological region anuran model was 0 68, and the *RMSE* was 0.88 species. Mean mapping unit elevation accounted for the largest proportion of the variation and was positively associated with species richness. The residuals for the Southern Semi-Arid Highlands anuran model were slightly larger than the residuals between the national model and atlas estimates of anuran species richness (fig 5a) No statistically significant model of urodele species richness could be developed from the available independent variables due to the limited variation in the dependent variable.

Climate trends

Amphibian species richness was strongly associated with several of the mean annual climate variables, and mean annual precipitation and mean annual temperature were statistically significant variables in 12 and 8 models, respectively (tab. 2). Increasing trends in annual mean temperature and precipitation were prevalent across much of the conterminous United States between 1960 and 1999 (fig. 6). Exceptions include decreasing mean annual temperature in parts of the Great Plains ecological region, and decreasing mean annual precipitation in the southeastern part of the Eastern Temperate Forests ecological region.

Discussion

At the national level, the model for anurans performed better than that for urodeles (fig. 5). Both models included mean annual precipitation as a strong variable for predicting patterns of richness. Kiester (1971) and Duellman & Sweet (1999) previously noted a strong correlation in the conterminous United States between amphibian species richness and mean annual rainfall. Partitioning the country by coarse-resolution ecological regions resulted in improved models for both anurans and urodeles. The residuals (model estimate minus atlas estimate) for the compilation of regional anuran and urodele models were much smaller than the residuals between national model and atlas estimates of anuran and urodele species richness in all mapping units (fig. 5). In several cases the R^2 for the regional models were less than that of the national model, but the residuals were also smaller. In general, temperature variables (mean annual mean and mean annual maximum) figured more strongly in anuran models, whereas precipitation (mean annual precipitation intensity) had greater explanatory value in urodele models. This makes sense from the perspective that there is no urodele counterpart to toads, hence, anurans are less restricted by arid conditions than are urodeles.

In general, trends in climate during 1960-1999 were toward wetter, warmer conditions for most of the conterminous United States. This could have provided more surface moisture availability for breeding habitat, and air and soil temperatures more amenable to regulating amphibian body temperatures throughout the year. Trends toward drier conditions in part of the southeastern United States and southwest Oregon may have resulted in reduced availability of breeding habitat in those areas.

This effort to model the relations between anuran and urodele species richness and mean annual climate in the United States capitalized on the strong dependence of amphibians on their external environment for internal hydrothermal regulation. A limitation of the approach was that it assumed that the climate experienced by amphibians was reflected by long-term climate statistics summarized at the county/subcounty level. In fact, amphibians interact with climate at multiple scales, and alter their behaviors in concert with microhabitat features (sun flecks, burrows, duff, vegetation cover, wetlands, etc.) to modify the effects of the broader-scale conditions. Therefore, the conditions represented by the data in this study likely addressed only the broadest effects of climate. For this reason, the statistical models presented

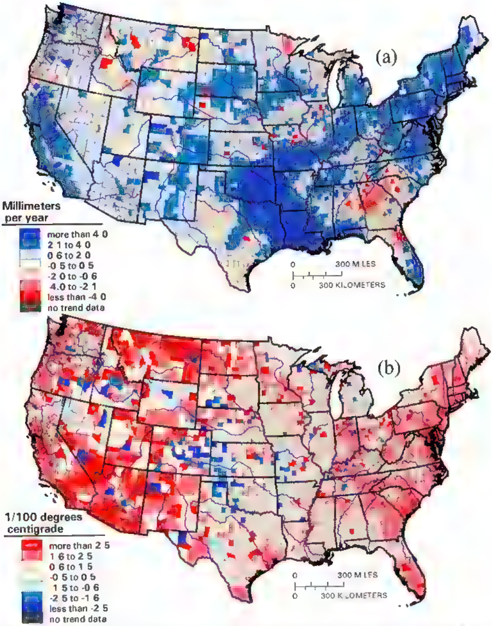

Fig. 6. Maps showing in the conterminous United States the trend for 1960–1999 in (a) annual mean precipitation and (b) annual mean temperature.

here were aimed at the general level of anuran and urodele richness, and were not aimed at predicting the fate of particular species.

Other explanatory variables may improve the ability to explain patterns of amphibian richness. For example, seasonal climate statistics may be more informative than annual statistics for certain measures, and additional landscape factors (e.g., current and historic land cover/use, hydrology, glaciation) and information such as evolutionary lineage could be very useful. Additionally, models could be developed at the family level, or for groups of species having similar life history or developmental characteristics.

The coarse-level ecological regions used for this study were somewhat problematic. Highly discontinuous mountain regions in the West often did not align well with county/subcounty units, so not all discontinuous portions of these regions were represented in the models. The largest regions (Eastern Temperate Forests, Great Plains and North American Deserts) included a lot of variation in temperature and moisture gradients. A finer level of regionalization (Level II regions defined in ANONYMOUS, 1997) may have been more appropriate, as it would have subdivided the largest regions, while leaving the smaller regions intact, however, the number of map units per region may have been insufficient for developing models for several of the regions at this level.

RÉSUMÉ

Les amphibiens occupent une grande diversité d'habitats sur la planète, mais leur richesse spécifique est plus élevée dans les régions aux climats humides et chauds. Nous avons modélisé les relations statistiques entre la richesse spécifique en anoures et urodèles et le climat annuel des Etats Unis continentaux, et comparé ces relations aux niveaux national et régional. Les variables modélisées ont été calculées pour des unités cartographiques correspondant aux contés ou aux sous-contés, et se sont appuyées sur des statistiques climatiques annuelles moyennes recueillies sur une période de 40 années (1960-1999), l'altitude moyenne et la surface des unités cartographiques, et des estimations de la richesse spécifique en anoures et urodeles. Les données climatiques ont été obtenues à partir de plus de 7500 stations météorologiques et ont été incorporées dans les données concernant les unités cartographiques au moyen de modèles de régression linéaire multiple. Les richesses spécifiques en anoures et urodèles ont été calculées à partir de l'atlas national de distribution des amphibiens préparé par l'Amphibian Research and Monitoring Initiative (ARMI) de l'United States Geological Survey. Le modèle de régression linéaire multivariée (MLR) national pour la richesse spécifique en anoures a un coefficient de détermination ajusté (R^2) de 0,64 et celui concernant les urodèles un R^2 de 0,45. Lorsque les Etats Unis sont divisés en régions écologiques grossières, on obtient des modèles pour les anoures dont les R^2 se répartissent entre 0,15 et 0,78 pour les anoures, et entre 0,27 et 0,74 pour les urodèles. En général, les modèles régionaux pour les anoures se sont avérés plus fortement influencés par des variables de température, tandis que les variables liées à la précipitation avaient plus d'influence sur les modèles pour les urodeles.

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